

The taxonomic status of *Hyperolius spatzi* Ahl, 1931 and *Hyperolius nitidulus* Peters, 1875 (Amphibia: Anura: Hyperoliidae)*

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* this paper is dedicated to Prof. Dr. Wolfgang Böhme, who's 1978 paper on the herpetology of Senegal induced our investigations presented herein.

Abstract. We herein re-investigate the taxonomic status of *Hyperolius nitidulus* Peters, 1875 and *H. spatzi* Ahl, 1931 by means of morphology, vocalization and genetic data. Both taxa are morphologically distinct, have different advertisement calls and differ genetically from each other by 5.1–5.6% sequence divergence in the investigated 16S rRNA gene. Based on these data we resurrect *H. spatzi* as a valid species and designate a lectotype for it. Both species occur in savannas of western Africa. *Hyperolius spatzi* is restricted to Senegambia and thus far known from Senegal and The Gambia. Its occurrence in Guinea Bissau and southern Mauritania seems likely. *Hyperolius nitidulus* ranges from Guinea and Mali eastwards into Nigeria and Cameroon. Records from the driest savannas in north-eastern Nigerian, Cameroon and the Central African Republic are doubtful and may actually refer to *H. pallidus* Mertens, 1940.

Key Words. Bioacoustics, biogeography, genetics, morphology, savanna, West Africa.

INTRODUCTION

Many species of the diverse African reedfrog genus *Hyperolius* Rapp, 1842 exhibit very variable color patterns (Schlötter 1971, 1975, 1999). Some of these color variations are age and sex specific (Schlötter 1967, Veith et al. 2009). As these frogs offer comparatively few other species specific morphological characters, this variability caused considerable taxonomic confusion in the past and resulted in the description of many taxa which are now regarded as synonyms (Frost 2010). One author in particular, Ernst Ahl, contributed to this chaos by describing many new species (e.g. Ahl 1931a, b), most of which proved to be invalid (Laurent 1961, Frost 2010). As the in-depth studies of Schlötter (1967, 1971, 1975) and others have shown, color and advertisement calls are the most reliable characters for identification of these species. Unfortunately, alcohol preserved *Hyperolius* specimens quickly lose color (and do not call). Therefore it is often difficult, if not impossible, to evaluate the status of older museum vouchers. Reliable locality data may be of help in some cases where taxa show allopatric distributions and/or different habitat requirements.

One group of savanna dwelling reedfrogs proved to be especially variable and consequently taxonomically complicated: the *Hyperolius marmoratus/viridiflavus* complex (Laurent 1951b, c, 1981; Schlötter 1971, 1999). These amazing reedfrogs have an outstanding natural history with annual population cycles and spectacular behavioral (Grafe et al. 2002), morphological and physiological adaptations, and altogether a unique life history strategy to survive the harsh and long dry seasons (Spieler 1997; Linsenmair 1998; Lampert & Linsenmair 2002 and literature cited therein). So far, they are the only tetrapods where sex change has been documented (Grafe & Linsenmair 1989; for literary use of this knowledge see Crichton 1991). To date, Laurent (1951a, 1976, 1983) and Schlötter (1971) undertook the most detailed morphological approach to disentangle the nomenclatory chaos of these widespread savanna dwelling frogs, which all share a similar morphology (short snout, very large vocal sac in males, transversal gular fold in females, extensive webbing) and call (xylophone like metallic calls; for summary see Schlötter 1971, 1999).

However, the mentioned studies of these frogs, using coloration and acoustics, did not provide much insight into their actual taxonomic status (see review by Wieczorek et al. 1998). Only more recently Wieczorek & Channing (1997) and Wieczorek et al. (2000, 2001) started to apply molecular techniques to disentangle the taxonomic chaos. In the course of their work in particular one member of the *H. viridiflavus*-complex/superspecies/species-group,

H. nitidulus Peters, 1875, was acknowledged species status, a decision previously already applied for mostly pragmatic reasons by e.g. Schiøtz (1967), Drewes (1984) and Rödel (1996, 2000). This widespread West African savanna frog was described by Peters (1875) from “Yoruba (Lagos)”, Nigeria. It was treated as a synonym of *H. marmoratus* by Boulenger (1882), as a synonym of *H. picturatus* by Loveridge (1955) and as synonym or subspecies

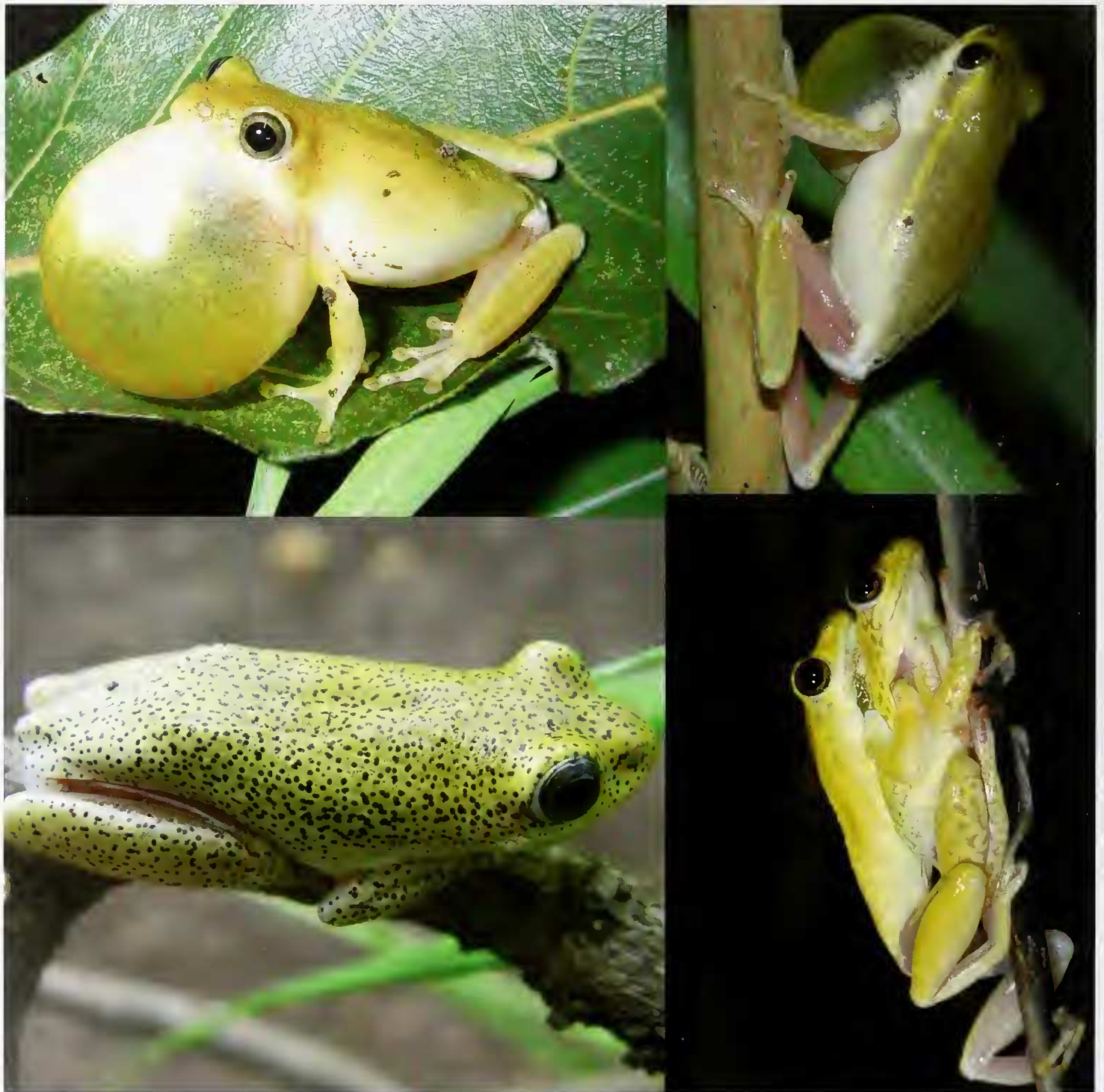


Fig. 1. Life coloration of *Hyperolius spatzi* and *H. nitidulus*; upper left: calling *H. spatzi* male from Sabodala, Senegal, remark uniform yellow color at night; lower left: daytime coloration of *H. spatzi* from Sabodala, Senegal, with numerous minute black points; upper right: calling *H. nitidulus* male from Pendjari National Park, northern Benin, remark dark lateral band; lower right: *H. nitidulus* couple from Lamto reserve, Ivory Coast, remark almost uniform yellow color of male and grey mottling on legs and on the flanks in the female.

Table 1. Morphological differences between *Hyperolius nitidulus* and *H. spatzi* based on data provided in the original descriptions and comments based on type specimens and additional material examined herein. Comments which are already deducible from types only, are given in *italic*.

Characters	<i>H. nitidulus</i>	<i>H. spatzi</i>	Comments based on types and additional material
Choanae	large, not hidden beneath edge of mandible	small, hidden below edge of mandible	<i>similar sized and well visible in both species</i>
Tongue	large, broad and heart-shaped	unusually small	<i>tongue in head width spatzi: 3.3 times; nitidulus: 1.7 times</i>
Snout (dorsal view)	roundish pointed	rounded	truncated in dorsal and lateral view in juveniles, a bit more rounded in adults of both taxa
Snout (lateral view)	flattened or roundish truncate	truncated	truncated in dorsal and lateral view in juveniles, a bit more rounded in adults of both taxa
Position of narins	slightly closer to snout-tip than to eye	in mid distance between eye and snout-tip	<i>in both species narins closer to snout-tip than to eye</i>
Position of heels when hind legs arranged to body at right angles	cover or surpass each other	in contact	<i>surpass each other in both taxa</i>
Dorsal skin	skin smooth, laterally smooth or with small warts	thick, almost leathery, rough, beset with many small smooth or rough warts	both taxa with rough skinned juveniles in dry season and smooth skinned adults in wet season
Male gular flap	absent	indistinct	present in both taxa
Dorsal color	yellow often with dark spots on back	chalk white or fine speckled with dark-brown	<i>H. spatzi</i> with white, brown or yellow back, regularly beset with small black spots; <i>H. nitidulus</i> never with such uniform pattern of black spots
Pattern on flanks	dark canthal and lateral stripe (continuous or broken), bordered white dorsally; below the stripe flanks marbled in dark grey and white	No pattern	<i>in H. spatzi</i> like on back; <i>H. nitidulus</i> with very distinct to rather indistinct black lateral band and dark spots
Body-length	28 mm	21 mm	adults of both species up to about 30 mm

of *Hyperolius viridiflavus* by many other authors (e.g. Laurent 1951a, c, 1961; Schiøtz 1971). The latter author also treated frogs described as *Hyperolius spatzi* Ahl, 1931 from Bakel-Kidira, Senegal (Ahl 1931a, b) as either belonging to *H. nitidulus* (Schiøtz 1967) or as a "subspecies" of *H. viridiflavus* (Schiøtz 1971). In his book, Schiøtz (1999) used the name "spatzi" as a vernacular name, describing "*H. viridiflavus*" populations of uncertain taxonomic status from Senegambia, whereas Rödel (2000) considered *H. spatzi* to represent a junior synonym of *H.*

nitidulus. However, already in the late seventies, Böhme (1978) revived the name *H. spatzi* for reedfrogs from Senegal, thus emphasizing their distinctiveness from other West African savanna populations. Recently Emms et al. (2006) adopted this view and reported *H. spatzi* from Gambia. Our recent studies of many *Hyperolius* populations at various West African savanna localities are the basis of a taxonomic reinvestigation of both taxa presented herein.



Fig. 2. Dorsal and ventral views of the types of left: *Hyperolius nitidulus* (ZMB 7729, holotype, adult female) and right: *H. spatzi* (ZMB 32602, lectotype, subadult male).

MATERIAL & METHODS

Morphological measurements were taken with a dial caliper (± 0.1 mm) and are given in millimeters. Webbing formulae follow the scheme of Rödel (2000). Museum vouchers originated from the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Museum für Naturkunde Berlin (ZMB; Appendix 2). Calls were recorded with a Sony WM-D6C tape recorder and a directional microphone (Sony ECM-Z157 and Sony ECU-959C9) or an EDIROL R-09 24bit digital recorder (sample rate: 44.1 kHz, record mode: way_24bit, microphone ECM-950). These calls were analyzed with the program Avisoft SAS Lab Pro 4.5 (R. Specht, Berlin, Germany). For sequence comparisons, we analyzed 247 base pairs (bp) of the mitochondrial 16S ribosomal RNA gene from *Hyperolius spatzi* (ZMB 74280, GenBank HQ113098; Senegal, Sabodala) and *Hyperolius nitidulus* (ZMB 74884, Gen-

Bank HQ113099, Sierra Leone, Tingi Hills; no voucher, GenBank HQ113100, Ivory Coast, Mont Sangbé National Park, tissue without voucher). Further hyperoliid gene sequences were obtained from GenBank (Tab. 1). DNA extraction, amplification and sequence alignment followed the procedures as described in Rödel et al. (2009). Uncorrected pairwise sequence divergence was calculated using PAUP*4b10 (Swofford 2002).

RESULTS & DISCUSSION

Morphological comparison. A major problem in using external morphological characters for determination of these frogs is their polymorphism. Schiøtz's (1963, 1967, 1971) described distinct color phases for many *Hyperolius* species, i.e. called F or A and J or B, respectively. The phase F/A of *H. nitidulus/spatzi* refers to the adult/wet season pattern, whereas phase J/B is the juvenile or sub-adult dry season pattern. Young frogs in dry season condition have a rough, warty dorsal skin which is brown below 35°C and chalk white above this temperature (see figs. in Spieler 1997 and Rödel 2000). Adult frogs have smooth skin and a completely different dorsal color pattern (Fig. 1). These morphological differences are part of the amazing aestivation strategy of these frogs (see Linsenmair 1998; Rödel 2000 and literature cited therein).

According to the descriptions by Ahl (1931b) differences between *Hyperolius nitidulus* and *H. spatzi* would be those summarized in Tab. 1 (compare also translations of the original descriptions provided in Appendix 1). Major differences between the descriptions of *H. nitidulus* and *H. spatzi* consist in the fact that the description of the former is based on an adult female, whereas the description of the latter is based on a series of subadult frogs in dry season condition (Fig. 2).

Schiøtz (1967, 1971, 1999) mentioned differences between various West African *H. nitidulus* populations, including a cline in pattern from Sierra Leone (few and small spots on flanks) to Cameroon (broad lateral band; same cline in pattern on the lower legs). He also observed an hour-glass pattern and a dark vocal sac in frogs from Sierra Leone (likewise present in some juveniles in northern Ivory Coast, see Rödel 2000). Our specimens from Sierra Leone neither differed in coloration nor in genetics (see below) from e.g. *H. nitidulus* populations from northern Ivory Coast. Schiøtz (1971) further mentions that frogs from drier northern savannas are more uniform grayish colored, whereas more southern ones, i.e. from the humid savanna types, exhibit a distinct pattern. The latter differences might be related to age. Rödel (2000) reported that older specimens are more distinctly colored. As adult *H. nitidulus* are unable to survive the dry season, all popu-

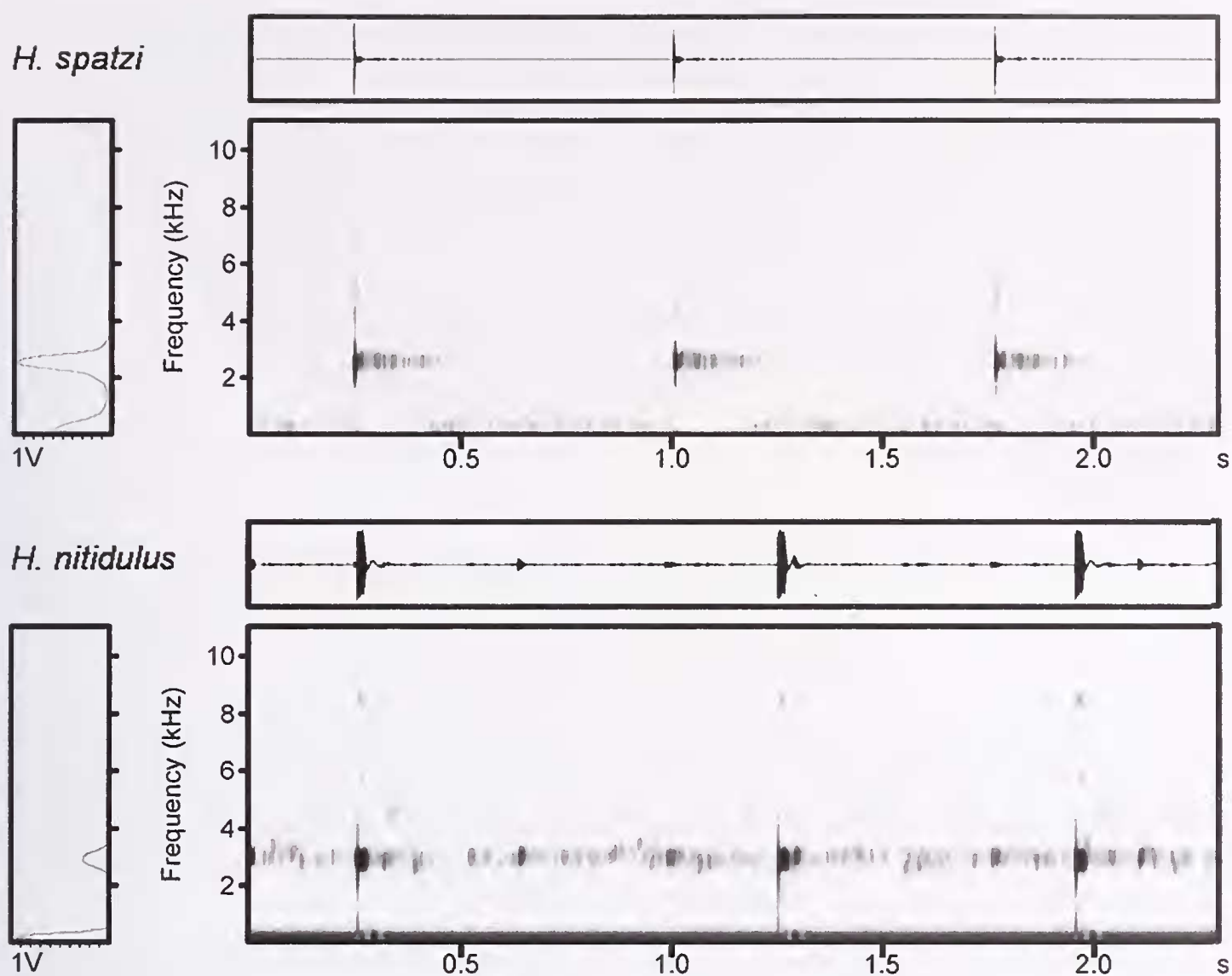


Fig. 3. Waveforms, spectrograms and energy plots of the advertisement calls of *Hyperolius spatzi* (above) and *H. nitidulus* (below; compare Tab. 2). The *Hyperolius spatzi* male from Sabodala, Senegal, was recorded in a terrarium. The *Hyperolius nitidulus* was recorded at a savanna pond in Comoé National Park, Ivory Coast. The background noise is a chorus of other *H. nitidulus* males.

lations are annual (Linsenmair 1998). In more humid savannas, the wet season lasts longer and frogs may reach older ages (and thus potentially a more colorful pattern).

Almost all anatomical differences (position and size of choanae, position of narins, size, shape, length of extremities, head width) deducible from Ahl's (1931a, b) descriptions (compare Tab. 1) are identical among both taxa (for specimens investigated see Appendix 2). Both species have very short, rounded snouts, females possess a typical gular fold and males have very large vocal sacs with a large but diffuse whitish yellow gular flap (gland). Juveniles are often almost indistinguishable. *Hyperolius nitidulus* juveniles show clear dorsolateral bands or an hour-glass pattern shortly after metamorphoses (see figs. in Rödel 2000). In dry season conditions they are uniform

brown or white. Juvenile *H. spatzi* in dry season conditions are white with many small black dots, the latter sometimes being indistinct. In contrast, adult frogs are distinctively colored. The dorsal surfaces of *H. spatzi* are chalk-white to yellow, densely beset with tiny black spots, whereas *H. nitidulus* is brownish or yellowish with black spots and has black lateral lines and spots (plate 18 in Leaché et al. 2006). *H. nitidulus* has white, yellow or reddish ventral surfaces, whereas these surfaces are exclusively yellow in *H. spatzi* (see fig. 2f in Emms et al. 2006). The hidden parts of legs are pinkish to blood red in both species (Fig. 2 and figs. 430 & 431 in Schiötz 1999, figs. in Rödel 2000). Generally, females of *H. nitidulus* have a more distinct lateral black pattern than males, which can be almost uniform brown (Fig. 1 and figs. in Rödel 2000). At night, males of both taxa appear uniform yellowish.

Table 2. Characteristics of the advertisement calls of *Hyperolius spatzi*, recorded in Sabodala, Senegal, and *H. nitidulus*, recorded in the Comoé National Park, Ivory Coast and Mount Nimba, Guinea (Fig. 3). Differences of call length, main frequency and time between calls have been tested by comparing mean values of five males of each species (Wilcoxon test).

	Call length [sec]	Frequency [Hz]	Inter-call intervals [sec]
<i>H. spatzi</i>	mean	0.08	1.12
	sd	0.04	0.80
	N (males)	5	5
	N (calls)	25	25
	mean	0.02	2927.6
<i>H. nitidulus</i>	sd	< 0.01	85.1
	N (males)	5	5
	N (calls)	25	25
	mean	0.02	2927.6
	sd	< 0.01	85.1
<i>W</i>	616	26	218
<i>P</i>	< 0.0001	< 0.0001	0.4756

Usually, the pattern in *H. nitidulus* remains vaguely visible. The only morphological difference detected by us (herein confirming Ahl 1931a, b), is the size and shape of the tongue. *Hyperolius spatzi* usually have comparatively smaller and narrower tongues than *H. nitidulus*, whose tongue is broad and almost heart-shaped. This is also visible in the type specimens of both species.

Acoustics. The advertisement call of both taxa is a single, pure, metallic and very loud tone (Fig. 3). Choruses of both species resemble xylophones or bells. Although superficially similar, advertisement calls of both taxa showed significant differences. The call of *H. spatzi* was of comparatively longer duration and lower frequency (Tab. 2). The small sample size and the relatively slight differences in call characteristics urge for some caution in their interpretation. However, the acoustic results are not contradicting the specific distinctiveness of *H. nitidulus* and *H. spatzi*.

Genetics. The genetic distances in the investigated fragment of the 16S RNA gene between *Hyperolius spatzi* (N=1) and *H. nitidulus* (N=3, originating from Sierra Leone and Ivory Coast) ranged from 5.1–5.6%. The mean distance between *H. spatzi* and various other members of the *H. viridiflavus/marmoratus*-complex (N=33; including *H. nitidulus*) was 5.9% (± 1.1 SD; range: 3.6–8.7%). The lowest distance was present in comparison to a *H. viridiflavus angolensis*, the highest to a *H. viridiflavus viridiflavus* sample (sequences from GenBank, compare Tab. 3). Mean

genetic distances between *H. spatzi* and nine other *Hyperolius* species was 18.7% (± 3.9 sd; range: 11.2–23.2%). The lowest distance present occurred in comparison to *H. fusciventris*, the highest to a *H. cinnamomeoventris* sample (compare Tab. 3).

Based on genetic data (12S and 16S), Wieczorek et al. (2000, 2001) recognized *H. nitidulus* as being distinct on the species level from other members of the *H. viridiflavus* group. Altogether they accepted ten species within this group of which *H. nitidulus* was most distinct (within intraspecific genetic variation 0.7–4.8%; between clade variation 2.4–10.0%; Wieczorek et al. 2001). Our data confirm their results and speak in favor of likewise recognizing *H. spatzi* as a distinct species.

Distribution. *Hyperolius nitidulus* occurs in humid to dry savannas of West Africa (Fig. 4; Lamotte 1966; Schiøtz 1967, 1999; Rödel 2000). Laurent's (1951c) doubts concerning the type locality of *H. nitidulus* were rejected by Schiøtz (1963), by explaining that savanna exists at the type locality, and thus also suitable habitats for *H. nitidulus*. Records have been published for Benin (Nago et al. 2006), Ghana (Schiøtz 1964a, 1967; Hoogmoed 1980; Hughes 1988; Rödel & Agyei 2003; Leaché 2005; Leaché et al. 2006), Burkina Faso (this paper), eastern and central Guinea (Laurent 1951a, c; Schiøtz 1967; Rödel et al. 2004; Hillers et al. 2006, 2008; Greenbaum & Carr 2005), Ivory Coast (Laurent 1951c; Lamotte & Perret 1963; Barbault 1967, 1972; Lamotte 1967; Schiøtz 1967; Vuattoux

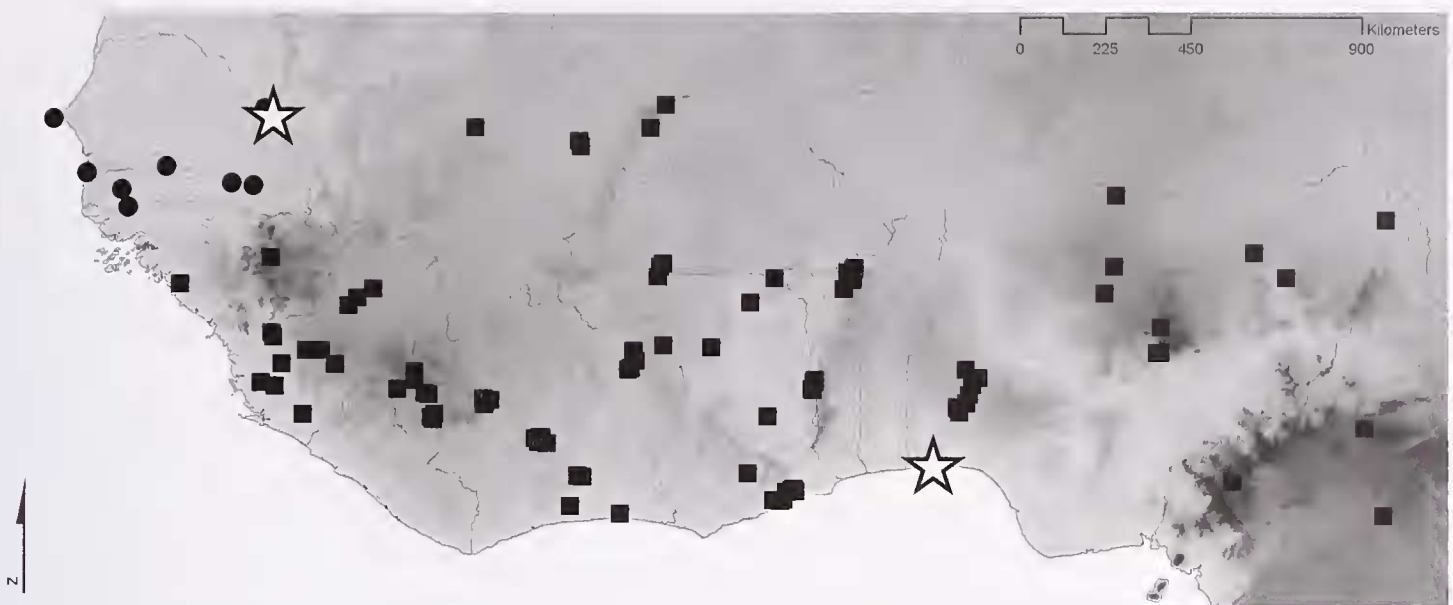


Fig. 4. Known distributions of *Hyperolius spatzi* (circles) and *H. nitidulus* (squares) based on museum and literature records (compare text and Appendix 2); stars indicate positions of type localities of *H. spatzi* (Senegal) and *H. nitidulus* (Nigeria). The north-westernmost record of *H. nitidulus* in Nigeria may refer to *H. pallidus*, southern and central Cameroonian populations are usually referred to two *H. nitidulus* subspecies (compare text and fig. 428 in Schiøtz 1999).

1968; Euzet et al. 1969; Rödel 1996, 1998, 2000, 2003; Spieler 1997; Linsenmair 1998; Rödel & Spieler 2000; Rödel & Ernst 2003; Adeba et al. 2010), Mali (Schiøtz 1967), Nigeria (Schiøtz 1963, 1966, 1967; Walker 1968; Onadeko & Rödel 2009), Sierra Leone (Schiøtz 1964b, 1967; Lamotte 1971), and Togo (Bourgat 1979; Segniagbeto et al. 2007).

Hyperolius spatzi, as defined herein, has been recorded from Senegal (Boettger 1881, as *H. cinctiventris*; Loveridge 1956; Schiøtz 1967; Lamotte 1969; Miles et al. 1978, listed as *H. nitidulus*; Ahl 1931a, b; Böhme 1978), and The Gambia (Andersson 1937 as *H. sp.*, but unambiguous description provided; Barnett & Emms 2005 as *H. nitidulus*; Emms et al. 2006). A record from Guinea was actually based on *H. nitidulus* (Hillers et al. 2006; see Appendix 2). Schiøtz (1971) recognized “*H. viridiflavus spatzi*” as a taxonomic unit occurring in Senegambia and provides a map, indicating the distribution of *H. spatzi* and *H. nitidulus*, respectively (fig. 42 in Schiøtz 1971). Padi-al & de la Riva (2004) believed that *H. nitidulus* and *H. viridiflavus* may occur in southern Mauritania. *Hyperolius viridiflavus (sensu stricto)* certainly does not occur in western Africa, including Mauritania. *Hyperolius nitidulus* might reach eastern Mauritania and it seems very likely that *H. spatzi* might be a part of the Mauritanian fauna, as is indicated by the close proximity of the type locality of this species to the boarder of Mauritania (Fig. 4).

Mountains and rivers can act as potential barriers between taxa (e.g. Li et al. 2009, for contrasting results see Gascon et al. 1998). In this case, the Gêba and Corubal rivers

along the border between Guinea-Bissau and Guinea, might fulfill such a role. It is also possible that the northern foothills of the Fouta Djallon serve as an altitudinal barrier. However, more data from Equatorial Guinea, westernmost Guinea, eastern Senegal, western Mali and Mauritania would be needed to clarify the exact limits of the species’ ranges.

The distribution of *H. nitidulus* in Central Africa is more complicated. The species is listed as *H. viridiflavus* (subspecies *H. v. nitidulus*, *H. v. pallidus*) for Cameroon, the Central African Republic and the Democratic Republic of Congo by Frétey & Blanc (2000). In northern Cameroon and adjacent north-eastern Nigeria, Chad and the Central African Republic (Joger 1990), *H. nitidulus* may be replaced by *H. pallidus* which was described by Mertens (1940) from dry northern Cameroon (Poli near Garua) and which has been treated by Perret (1966) as a full species, and by Schiøtz (1971) and Amiet (1973) as a subspecies of *H. nitidulus*. From Cameroonian savannas, situated a bit further south, two *H. nitidulus* subspecies have been described by Perret (1966). *Hyperolius n. bangwae* occurs in elevated savannas, i.e. Bamenda, Bamiléké, Adamaoua, whereas *H. n. aureus* is said to occur in the drier northern savannas and semi-deserts (Perret 1966; compare e.g. Böhme & Schneider 1987 for some records). This view was adopted by Schiøtz (1971) and Amiet (1973). The latter provided arguments for the treatment of these taxa as subspecies of *H. nitidulus*, i.e. Cameroonian frogs differ from typical *H. nitidulus* by slightly smaller size and slightly duller coloration. The voices are “as good as identical” (Amiet 1973). More recently, Amiet thought that all

Table 3. Genetic distances between *Hyperolius spatzi* (ZMB 74280; GenBank #: HQ113098) and other *Hyperolius* species. Uncorrected p-distances are based on 247 base pairs of mitochondrial 16S ribosomal RNA. Values for *H. nitidulus* are given in bold.

Genus	Species	„Subspecies“	GenBank #	p-distance
<i>Hyperolius</i>	<i>chlorosteus</i>		FJ594076	0.214
<i>Hyperolius</i>	<i>cinnamomeoventris</i>		FJ594077	0.232
<i>Hyperolius</i>	<i>concolor</i>		FJ594078	0.203
<i>Hyperolius</i>	<i>fusciventris</i>		FJ594080	0.112
<i>Hyperolius</i>	<i>guttulatus</i>		FJ594082	0.133
<i>Hyperolius</i>	<i>horstocki</i>		AF282410	0.199
<i>Hyperolius</i>	<i>kivueensis</i>		AF282409	0.183
<i>Hyperolius</i>	<i>naustus</i>		AF215442	0.219
<i>Hyperolius</i>	<i>nitidulus</i>		HQ113099	0.051
<i>Hyperolius</i>	<i>nitidulus</i>		HQ113100	0.051
<i>Hyperolius</i>	<i>nitidulus</i>		AF282435	0.056
<i>Hyperolius</i>	<i>picturatus</i>		FJ594090	0.186
<i>Hyperolius</i>	<i>viridiflavus</i>		AF215440	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>		AF215441	0.061
<i>Hyperolius</i>	<i>viridiflavus</i>		AY323920	0.077
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>angolensis</i>	AF282411	0.036
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>albofaciatus</i>	AF282433	0.065
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>aposematicus</i>	AF282412	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>argentovittis</i>	AF282431	0.046
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>bayoni</i>	AF282413	0.082
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>broadleyi</i>	AF282414	0.071
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ferniquei</i>	AF282416	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ferniquei</i>	AY603987	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>glaudicolor</i>	AF282417	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>goetzi</i>	AF282418	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>mariae</i>	AF282419	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>mariae</i>	AF282420	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>marginatus</i>	AF282430	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>melauoleucus</i>	AF282432	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pantheriinus</i>	AF282425	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pitnaui</i>	AF282426	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>maruoratus</i>	AF282421	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ngorongoro</i>	AF282423	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>oumatostictus</i>	AF282424	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pyrrhodictyon</i>	AF282434	0.046
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>rhodesianus</i>	AF282427	0.038
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>rubripes</i>	AF282436	0.062
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>swynnertoni</i>	AF282415	0.071
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>taeniatus</i>	AF282422	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>verrucosus</i>	AF282428	0.062
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>viridiflavus</i>	AF282429	0.087

three Cameroonian taxa are subspecies of *H. viridiflavus*, i.e. the highlands of western Cameroon and the Adamaoua plateau being inhabited by *H. v. aureus* (and possibly *H. v. bangwae*), and populations occurring in northern Cameroon (mid-Sudanian, Sudano-Sahelian and Sahelian zones) belong to *H. v. bangwae* and *H. v. pallidus* (J.-L. Amiet pers. comm.).

Conclusions. Our investigations on the type specimens, as well as on additional vouchers, revealed small but distinct morphological (mostly color pattern; tongue shape and size), significant acoustic and large genetic differences (16S gene). Especially the genetic differences are clearly within the range that is thought to be species specific in anurans (Vences et al. 2005a, b; Rödel et al. 2009; Vieites et al. 2009). Our results thus speak in favor of recognizing both taxa as distinct species. A contradicting argument was seen in the very complicated situation of a large variation of color patterns between and within populations of the *Hyperolius viridiflavus/marmoratus* species group(s). Schiøtz (1999) thus questions an approach where the taxonomy for only a small part of the continent would be resolved. However, in West Africa it is possible to assign these frogs to particular names and we thus do not see a reason for avoiding it. We therefore herein resurrect the species status of *H. spatzi*, designate a lectotype from the series of syntypes and redescribe the species based on type and new material.

REDESCRIPTION OF *HYPEROLIUS SPATZI* AHL, 1931.

ZMB 32602 (lectotype; Fig. 2), 74853-74876 (paralectotypes, formerly all ZMB 32602), all from Bakel-Kidira, Senegal, coll. Spatz.

Description of lectotype (all measurements in mm). Subadult frog (male, vocal sac barely developed?); short, compact body; snout-vent length 19.2; head width 7.3, head length 6.9, thus head wider than long; snout short and truncated in dorsal and lateral view; narins angular narrow slit, closer to snout-tip than to eye; tympanum hidden; transversal gular fold; tongue small, narrow, almost parallel and notched anteriorly, tongue width 2.3, tongue length 3.2, tongue 3.3 times in head width; choanae small and round, close to edge of mandible but well visible; dorsal skin slightly granular; belly granular (medially dissected); ventral skin on thighs near vent granular, remaining ventral parts of hind limbs smooth; finger and toe tips enlarged to discs; relative lengths of fingers: 1<2<4<3; basal webbing between fingers; femur length: 8.4; tibia length: 10.4; foot incl. longest toe: 14.0; relative lengths of toes: 1<2<3<5<4; webbing formula: 1 (0), 2 (1.5–0), 3 (1.5–0.5), 4 (1–0), 5 (0); subarticular tubercles on fingers

and toes not very prominent. Dorsal surfaces chalk white, densely beset with minute black points; ventral skin on thighs near vent white, remaining parts of thighs and ventral parts of shanks, feet, inner parts of forelimbs, ventral part of hands and fingers fleshy colored.

Variation. Series of paralectotypes almost indistinguishable from lectotype, exclusively subadult frogs in dry season conditions; dorsal skin partly more or less granular than in lectotype; black points on white ground sometimes more distinct or sometimes almost absent. Further material (see Appendix 2) exhibit the following variation: Male snout-vent length: 27.0–31.3 (N= 6); female snout-vent length 30.6 (N= 1); snout shape of adult frogs in dorsal and ventral view slightly more rounded than in juveniles; adults of both sexes in ethanol with dorsal surfaces (incl. upper side of thighs) with brownish ground color (composed of small, very dense brownish points), many very distinct black spots; black spots sometimes a bit more abundant on flanks than on back; some specimens with black spots on throat; others with uniform clear ventral surfaces; tongue in almost all specimens small and comparatively narrow (exception: ZMB 74279). Adult animals in life brownish to yellow with very distinct black spots. These may be not visible during night. Venter yellow.

Acknowledgements. We thank SRK Consulting (Canada) and the Oromin Exploration Ltd. for financial and logistic support for conducting a survey in south-eastern Senegal which enabled us to collect and sequence several specimens of *Hyperolius spatzi*; and the authorities in various West African countries for the respective research, collection and export permits. J. Köhler provided valuable comments on the manuscript. This study is part of the BIOLOG-program of the German Ministry of Education and Science (BMB+F; Project BIOTA-West III, amphibian project, 01LC0617J).

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APPENDIX 1.

Translations of the original descriptions of *Hyperolius nitidulus* by Peters (1875) and *Hyperolius spatzi* by Ahl (1931a):

Hyperolius nitidulus (Fig. 2): “Body shape equals that of *H. marmoratus*. Snout same length as eye. Tympanum hidden. Belly and ventral surfaces of thighs granular. The outer two fingers and the forth toe, with the exception of the two most distal phalanges, webbed. Dorsally purple grey, shanks likewise colored, whereas the thighs seem to be uncolored. A black band from nose through eye to belly, there band dissolving into black spots on white background; upper lip, flanks below this band, anal region, upper surfaces of forearms, outer and inner edge of shanks and external side of foot to toe tips (in ethanol) white with black spots, which plus/minus fuse. Total length 28 mm; head: 8 mm; head width: 8.5 mm; forearm: 19 mm; hand with 3rd finger: 7 mm; hind leg: 44 mm; foot with fifth toe: 20 mm. From Yoruba (Lagos). [comment added: referring to ZMB 7729, holotype]” Plate 3 (figures 4 and 4a) in Peters (1875) figures the typical wet-season color pattern of this species.

Hyperolius spatzi (Fig. 1): “stocky body shape; vomerine teeth absent; choanae very small, hidden below edge of mandible; tongue unusually small, notched posteriorly; large head, app. 1/3 of body length, wider than long; snout rounded, truncate in lateral view, not or only slightly surpassing mouth, as long as eye, much shorter than distance between anterior corner of eyes, slightly longer than high; *canthus rostralis* rounded but distinct; loreal region vertical, only slightly eoneave; nares in mid distance between eye and snout-tip; inter-narial distance slightly narrower than inter-orbital distance, the latter twice as wide as upper eyelid; tympanum hidden beneath skin.

Robust fingers, 1/3 to 1/2 webbed; well developed discs; 1st finger shorter than second, second shorter than fourth, which is slightly surpassed by the 3rd finger; 3rd finger as long as snout; subarticular tubercles moderately large, not prominent. Webbing on feet complete with the exception of 4th toe where the last phalanx is without webbing; discs as large as those on fingers; 5th toe slightly longer than 3rd; external metatarsalia tightly fused, tarsal fold absent; very small inner metatarsal tubercle; outer metatarsal tubercle lacking; no tarsal tubercle; subarticular tubercle small, moderately distinct. Tibio-tarsal angle surpasses eye or reaches snout-tip. Femur shorter than tibia, the latter 3.5–4 times longer than wide and twice or slightly less times in body length, longer than foot; heels in contact when hind legs arranged to body at right angles.

Dorsal skin thick, almost leathery, rough, beset with many small smooth or rough warts; ventrum granular; distinct postgular and postpectoral folds; no temporotemporal fold; males with subgular vocal sac and a small, indistinct gular flap.

Coloration in alcohol dorsally chalk white or, rarer, fine speckled with dark-brown. Venter white. Ventral parts of thighs and inner parts of shanks flesh-colored (presumably red in life). No markings at all.

Body length 21 mm. Bakel-Kidira (Upper Senegal region). 26 specimens, Bakel-Kidira, Spatz leg., types [comment added: ZMB 32602, lectotype; 74853-74876, paralectotypes; formerly all ZMB 32602]. The species is named to honor the collector, the well know researcher Spatz, whose collecting activities resulted in a large number of valuable reptiles and amphibians, stored in the Berlin museum.”

APPENDIX 2.

Voucher specimens, including types, of *Hyperolius spatzi* and *H. nitidulus* in the ZMB and SMNS collections.

***Hyperolius nitidulus*. Benin:** ZMB 74896-74898, Pendjari National Park, Sudan savanna, October 2003, coll. Olaf Grell; ZMB 74890, Pendjari National Park, Tangieta, savanna, N 10°38.317', E 01°15.746', 1 September 2004, coll. G.A. Nago & M.-O. Rödel; **Burkina Faso:** ZMB 74893-74894, Dano, small river in savanna, N 11°14'16.8", W 03°01'24.1", 22 October 2003, coll. T. Moritz; **Ivory Coast:** SMNS 8995.1-2, Ananda, 1993, coll. M.-O. Rödel; SMNS 9680.1-2, Bondoukou, 1996, coll. K. Kouadio; ZMB 74888 & SMNS 8967.1-7, Comoé National Park, savanna, June 1996, coll. M.-O. Rödel; ZMB 74886, Mont Sangbé National Park, Mare Soumarou, island forest in the savanna, pitfall trap, dry season 2001, coll. G. Gbmalin & Y. Cesar; **Guinea:** ZMB 74895, Mont Béro Classified Forest, savanna, N 08°08'30.9", W 08°34'09.6", 1 December 2003, coll. M.A. Bangoura & M.-O. Rödel; ZMB 74891-74892 Nimba Mountains, savanna Séringbara, with big ponds, close to village, N 07°36.181', W 08°29.769', 18 May 2006, coll. T.N.-S. Loua & A. Hillers; ZMB 74889, Pic de Fon/Simandou range, Banko, savanna, 11 July 2004, coll. M.A. Bangoura & K. Kamara; ZMB 74882, Boké Préfecture/Kolabou, swampy area in secondary forest island, N 10°45.075', W 14°27.040', 23 & 24 April 2005, coll. M.A. Bangoura & A. Hillers (originally listed as *H. spatzi* in Hillers et al. 2006); **Nigeria:** ZMB 7729 (holotype), Yoruba (Lagos), coll. Krause; **Sierra Leone:** ZMB 74884-74885, Tingi Hills, big pond with a few trees around and swampy area in savanna, N 08°51.047', W 10°46.502', 427 m a.s.l., 5 June 2007, coll. J. Johnny & A. Hillers; **Togo:** ZMB 39028, station Sokode, coll. Schröder.

***Hyperolius spatzi*. Gambia:** ZMB 74877, Abuko Nature Reserve, savanna, 2005, coll. L. Barnett & C. Emms; **Senegal:** ZMB 32602 (lectotype), 74853-74876 (paralectotypes, formerly all ZMB 32602), Bakel-Kidira, coll. Spatz; ZMB 74279, Sabodala, ponds and puddles in degraded farmbrush savanna next to Oromin camp, N 13°09.368', W 12°06.882', 12 September 2009, coll. A. Hillers & Y. Mané; ZMB 74280-74285, Sabodala, in and around big pond in farmbrush savanna/grassland, with some rocks, N 13°07.259', W 12°07.622', 7 September 2009, coll. A. Hillers & Y. Mané.

Received: 26.VII.2010

Accepted: 24.VIII.2010